

JAN 14 1994

A NEW SPECIES OF *EXTATOSOMA* GRAY
 (PHASMATODEA: PHASMATIDAE) FROM PAPUA
 NEW GUINEA, WITH REMARKS ON THE SPECIES IN
 THE GENUS

HARVARD
UNIVERSITY

Beccaloni, G. W., 1993. A new species of *Extatosoma* Gray (Phasmatodea: Phasmatidae) from Papua New Guinea, with remarks on the species in the genus. — *Tijdschrift voor Entomologie* 136: 113-123, figs. 1-16, tabs. 1-2. [ISSN 0040-7496]. Published 10 December 1993.

Extatosoma carlbergi sp. n. (Phasmatidae), is described from Papua New Guinea. The biology, ecology and distribution of this and the three other species of *Extatosoma* Gray is discussed and a hypothesis is advanced to explain the discrete altitudinal ranges of the two New Guinean species. The phylogenetic relationships of the species are considered and a key to the adult females is presented.

G. W. Beccaloni, Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK.

Key words. — Phasmatodea, Phasmida, *Extatosoma*, New Guinea, Australia, biology, ecology, distribution, phylogeny.

The genus *Extatosoma* is widely known due to familiarity with an Australian species, *E. tiaratum* (MacLeay 1826). This is one of the stick-insects most commonly cultured by amateur enthusiasts (Bragg 1991) and it is also a popular laboratory animal on which many physiological, behavioural and morphological studies have been conducted (for references see Carlberg 1983, 1987a).

Two other species are currently recognised as belonging to the genus: *E. bufonium* Westwood, 1874 from Australia and *E. popa* Stål, 1875 from New Guinea. Another nominal species, *E. elongatum* Froggatt, 1922, was synonymised with *E. bufonium* by Vickery (1983). The holotype of *E. bufonium* (in the Hope Entomological Collection, Oxford, UK) is a penultimate (?) instar female nymph, not a male as stated by Vickery (1983), and Froggatt (1922) based *E. elongatum* on the adult female of this species. A third, as yet undescribed, species may exist in the vicinity of Brisbane, Queensland, Australia (P. D. Brock, in prep.). The adult female of this taxon (fig. in Wilson 1991) is superficially similar to *E. tiaratum* in appearance, while the egg resembles that of *E. bufonium*.

Both *E. popa* and *E. bufonium* are poorly known and only the former species has been cultured in captivity (Harman 1985). The males of these two species have not been figured or formally described, although Harman briefly noted that the male of *E. popa* can be

distinguished from that of *E. tiaratum* by its clear wings and a white dot behind its head. From personal observation of a series of preserved adult male *E. popa* cultured by Harman and deposited in the BMNH, it is evident that the 'white dot' referred to is in fact a pale v-shaped marking on the mesonotum, similar to that possessed by the adult female of this species.

The existence of a second New Guinean species of *Extatosoma* was first suggested in print by Harman (1985) who stated that there is '....another species [of *Extatosoma*] which occurs in the mountainous regions of Papua New Guinea. I have seen a number of specimens in the collection at the Wau Ecology Institute Museum'. During July and August of 1990 the author led an Imperial College (University of London) expedition to Papua New Guinea (PNG). For the first four weeks we were based at the Wau Ecology Institute (WEIC) and the author took the opportunity to investigate Harman's claim. Three adult females of an undescribed *Extatosoma* were present in the WEIC collection, together with a note stating that the taxon was new.

A reward was offered to two Papuan youths to collect living specimens of this species and one day later an adult female (fig. 1) was received. This individual was placed in a cylindrical net cage on cut foodplant standing in water and was kept alive for twelve days for observation.

Despite further requests and a search of the locality



Fig. 1. *Extatosoma carlbergi* sp. n. – Holotype ♀ resting on twig of *Calliandra surinamensis* Benth.

from which the specimen had been collected, no other individuals were obtained. Several local Papuans who were interviewed stated that they were familiar with this species but that it was only rarely seen (more rarely than *E. popa*).

MATERIALS AND METHODS

The terminology used to describe eggs is after Clark (1976a), with the following additions and modifications : 'total egg length' is the length of the egg capsule plus the length of the operculum ; 'length of operculum' is the maximum length of the operculum from its base to its summit ; 'diameter of operculum' is the maximum diameter across the base of the operculum ; 'micropylar arm' is a new term given to the lateral extensions of the micropylar plate located on either side of the micropylar cup region ; 'length of micropylar arm' is the length of one micropylar arm measured from the centre of the micropylar cup to the apex of the arm; 'distance across micropylar arms' is the maximum distance between the tips of the micropylar arms ; 'height of micropylar mound' is the height with which the micropylar plate is raised above the surface of the egg capsule and is measured midway along the plate's length; 'chorionic membrane' is a new term given to the membrane or layer which covers the entire outer surface of the egg. This membrane expands and detaches from the egg surface if the egg is immersed in alkali (e.g. sodium hydroxide solution). The membrane is thinner and weaker around

the base of the operculum and the portion of membrane covering the operculum remains attached to it when it detaches on hatching of the egg. The eggs of all four *Extatosoma* are covered by a chorionic membrane, but it appears to be absent from the eggs of other stick-insect species (Clark 1976b); 'capitulum', in light of the recent discovery that this structure has a function analogous to the elaiosome of certain plant seeds, and acts as a handle which enables ants to carry stick-insect eggs back to their nests (Compton & Ware 1991, Hughes & Westoby 1992), the author proposes to restrict Clark's (1976a) definition to structures attached to and protruding from the surface of the operculum.

The coloration of *E. carlbergi* is described from slides of the living holotype taken on 'Kodachrome 64' slide film under natural lighting conditions. Specimens of *E. carlbergi* and *E. popa* collected by the author were killed by freezing and preserved by injection of embalming fluid (formula in Cogan & Smith 1974). Eggs (fully developed) were removed from the

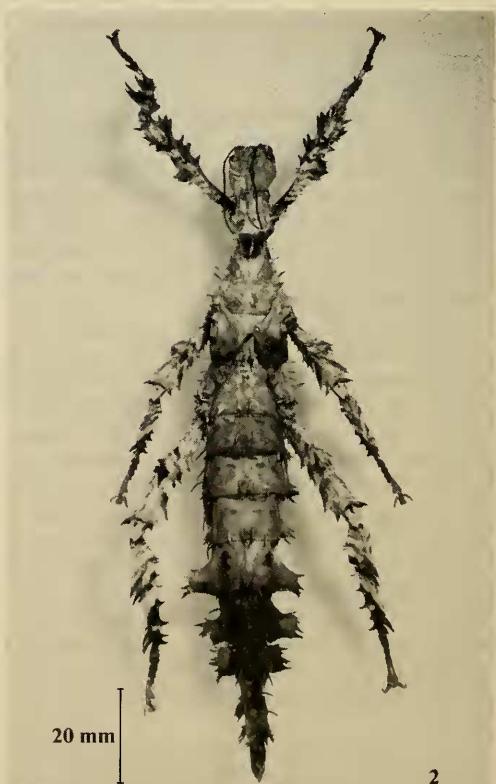
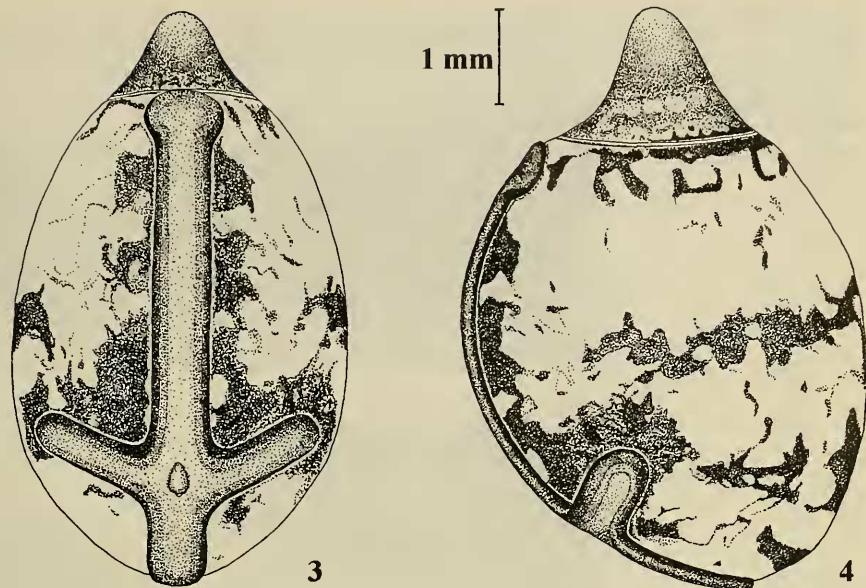


Fig. 2. *Extatosoma carlbergi* sp. n. – Holotype ♀, dorsal habitus.

Figs. 3-4. Egg of *Extatosoma carlbergi* sp. n. taken from ovipositor of holotype. – 3, dorsal view; 4, lateral view.



abdomen of the *E. carlbergi* holotype by first relaxing the specimen (in a sealed plastic box with damp tissue paper in the base) and then by softening a section of intersegmental membrane between tergites and sternites with 10% aqueous ammonia solution, so that an incision could easily be made and the eggs removed with forceps. The chorionic membrane was removed from eggs for study, by placing the eggs for c. 5 minutes in a 5% aqueous solution of sodium hydroxide at room temperature. Drawings were produced using a drawing tube on a Wild M5 stereomicroscope. All measurements are given in millimetres. Measurements of eggs (accurate to 0.01 mm) were made using an ocular micrometer, except for micropylar plate length, which because of the plate's curvature, was first drawn using a drawing tube and then measured using inelastic fishing line and a ruler. All other measurements (accurate to 1 mm) were taken from specimens using a pair of dividers and a ruler.

Abbreviations of depositaries

BMNH: The Natural History Museum, London, England; BPBM: Bishop Museum, Hawai'i; TPNG: Central Reference Insect Collection, Department of Agriculture and Livestock, Port Moresby, Papua New Guinea; FICB: National Forest Insect Collection, Forest Research Institute, Lae, Papua New Guinea; NHMN: Nottingham Natural History Museum, Nottingham, England; UPNG: University of Papua New Guinea, Port Moresby, Papua New Guinea; WEIC: Wau Ecology Institute, Wau, Papua New Guinea.

TAXONOMY

Extatosoma carlbergi sp. n.

(figs. 1-5, 8, 12-14)

Type material. – Holotype ♀: Papua New Guinea, Morobe Province, Wau, golf course, c. 1150 m, ex *Calliandra surinamensis* Benth., 14.vii.1990, G. W. Beccaloni (BMNH). – Paratypes: PAPUA NEW GUINEA: 2♀, Southern Highlands Province, Tari, 1600 m, ex *Casuarina*, 4.x.1963, R. Straatman (BPBM); 1♀ (fragmented), Chimbu Province, Karimui, 4.vi.1961, Gressitt (BPBM); 1♀, Morobe Province, Wantoat, feeds on *Casuarina*, 1.xii.1957, R. W. Paine (BMNH).

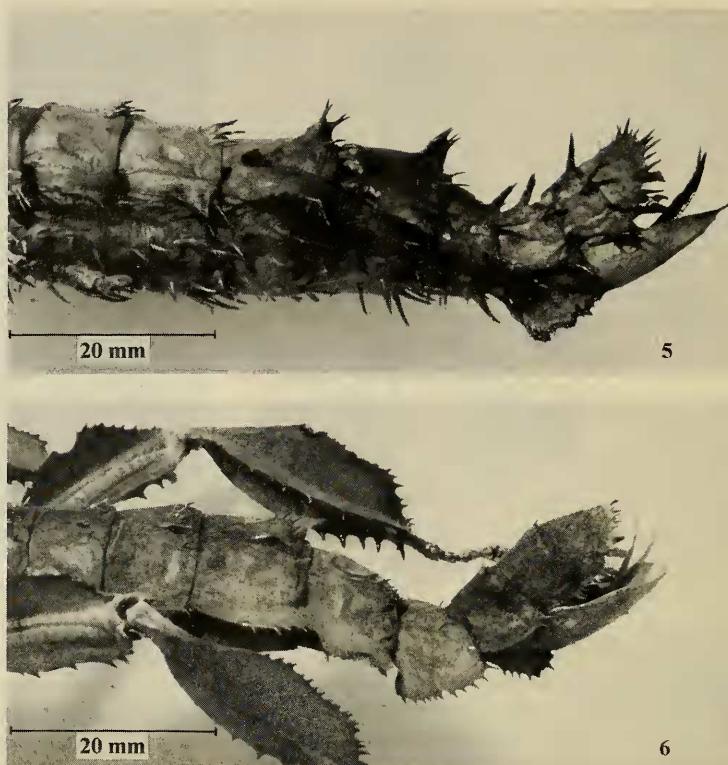
Additional material examined. – NEW GUINEA: 1♀, no other data (NHMN); PAPUA NEW GUINEA: 2♀, Southern Highlands Province, Pangia, defoliating *Casuarina oligodon*, 1.vi.1971, J. Lowien (FICB); 1♀, Southern Highlands Province, Pangia, found on *Casuarina* trees, 30.iv.1971, J. Wallis (TPNG); 2♀, no data (WEIC); 1♀ (nymph, penultimate? instar), Morobe Province, Wau, 1200 m, 14.x.1966, G. A. Samuelson (BPBM); 1♀, Morobe Province, Wau, 1100 m, collected on *Casuarina* sp., 10.xii.1974, A. D. Hart (WEIC); 1♀, Morobe Province, Wau, Wau Ecology Institute Office, 1150 m, 27.xi.1986, J. Somp (UPNG).

Description

Based on adult female holotype and four adult female paratypes. Measurements of selected structures given in table 1. Male unknown.

Female (adult). – Head typical for the genus; hypognathous with conical occiput. Occipital medial spines large and robust; four pairs anterior to crest and two pairs posterior to crest. A large lamellate compound spine present on either side of occipital

Figs. 5-6. Lateral views of abdomens of adult ♀ *Extatosoma* spp., showing spination on tergites 3-10. – 5, *Extatosoma carlbergi* sp. n. (holotype); 6, *Extatosoma tiaratum*.



crest. Eyes small and globular, situated anterolaterally. Ocelli indicated by slight swellings covered by integument. Antennae simple, with 25 segments ($n=2$). A large spine present between eyes and antennal sockets.

Pronotum elongate-rectangular, slightly rounded posteriorly. Spines around margin variable in size and number; a pair of large medial lamellate spines usually present on posterior third of segment.

Mesonotum with a well developed pair of pre-median spines and a large pair of compound lamellate spines situated between tegminal bases. Lateral borders with 3-6 large spines, the two directly above the tegminal bases often confluent basally. Tegmina reduced, lobose, extending to posterior margin of metanotum.

Metanotum with a pair of well developed lamellae above posterior margin. Wings rudimentary, extending into anterior third of first tergite.

Tergites one to nine bearing a pair of medial compound lamellate spines on the posterior third, with a well developed simple spine posterior and to either side of these. The lamellate spines on tergites five and six especially well developed (fig. 5); those on tergites seven to nine are sometimes simple. The posterolateral margins of tergites two to nine expanded laterally

and strongly serrated or spined. The anterolateral margin of the tenth tergite is similarly produced. Lateral expansions of tergites five to seven are c. twice the size of those on the other tergites. Tenth tergite usually with a pair of medial spines on posterior half and the hind margin has large posteriorly directed spines (fig. 5).

Supra-anal plate with large pair of posteriorly directed medial spines. Cercus 2.6 mm in length, bilobed, setose (fig. 14). Both structures concealed beneath tenth tergite.

Operculum keel-shaped, the anterior third ventrally expanded with a serrated edge (fig. 5). Sternites two to seven with many long to short irregularly arranged robust spines. A pair of double weakly confluent medial spines may be present posteriorly. Spination of sternites four to six reduced in comparison with that of sternites two to three. Meso- and metathoracic basisterna with few irregular short robust spines. Ventral margins of meso- and metathoracic episterna with long to short laterally or ventrally directed spines.

Fore femur with strongly serrated dorsal and lateral expansions. Fore tibia with dorsal expansion arcuate and ventral expansion denticulate (fig. 8). Proximal tarsomere of fore leg expanded into lobe

Table 1. Measurements of selected structures of type specimens and female (?) penultimate instar) nymph of *E. carlbergi*. All measurements in mm (accurate to 1 mm). ¹ excluding occipital spines; ² n = 1.

Structures measured (Lengths)	Holotype	Paratypes (n=4)	Nymph	
			$\bar{x} \pm SD$	Range
Body	128	129 \pm 9.9	116 - 140	70
Antenna	27	27 ²	—	11
Head ¹	19	19.5 \pm 1.3	18 - 21	11
Pronotum	9	10.5 \pm 1.3	9 - 12	5
Mesonotum	15	16.0 \pm 0.8	15 - 17	10
Metanotum	12	11.5 \pm 0.6	11 - 12	5
Fore femur	25	22.5 \pm 1.3	24 - 27	15
Median femur	20	20.3 \pm 1.0	19 - 21	11
Hind femur	30	28.8 \pm 1.0	28 - 30	15
Fore tibia	23	23.5 \pm 0.6	23 - 24	13
Median tibia	21	21.0 \pm 1.2	20 - 22	12
Hind tibia	32	32.8 \pm 1.7	31 - 35	16
Operculum	26	24.3 \pm 0.5	24 - 25	7

dorsally towards distal end. Dorsal surfaces of median and hind femora (figs. 12-13) with serrated expansion distally. Outer ventral margin serrated and expanded ventrally. Inner ventral margin spined and expanded distally. Dorsal expansions of hind tibia usually strongly arcuate (fig. 12), rarely weakly so (fig. 13); median tibia likewise. Inner and outer ventral margins of median and hind tibiae with large ventrally directed spines. Legs and body densely setose.

Coloration in life: Mesonotum with conspicuous v-shaped marking which is paler than rest of segment (this marking is usually white or cream in preserved specimens). Arms of 'v' extend from anterolateral corners of segment, with base of 'v' below middle of segment. Area between arms usually black or dark brown. Dorsal and ventral surfaces of body (including spines, tegmina and wings) pale green with darker green, white and black mottling; mirrored on each side of body. Intersegmental membranes cream to light brown. Legs with similar coloration to rest of body; dorsal surfaces with a higher incidence of larger black and dark green marks often arranged as transverse stripes; ventral surfaces (less so of fore legs) aposematically patterned with thick irregular black, ochreous and white transverse bands. Median and hind tibiae often with black predominating.

Nymph (female, penultimate ? instar). — Measurements given in table 1. Morphology similar to that of adult, except that wings not developed (small, c. 1.5 mm long wing buds present) and operculum is relatively shorter; not extending beyond posterior margin of ninth tergite and not covering the supra-anal plate or cerci. Coloration in life presumed similar to that of adult, as coloration is similar to that

of the preserved adult specimens examined (i.e. with light to dark brown replacing pale green ground colour).

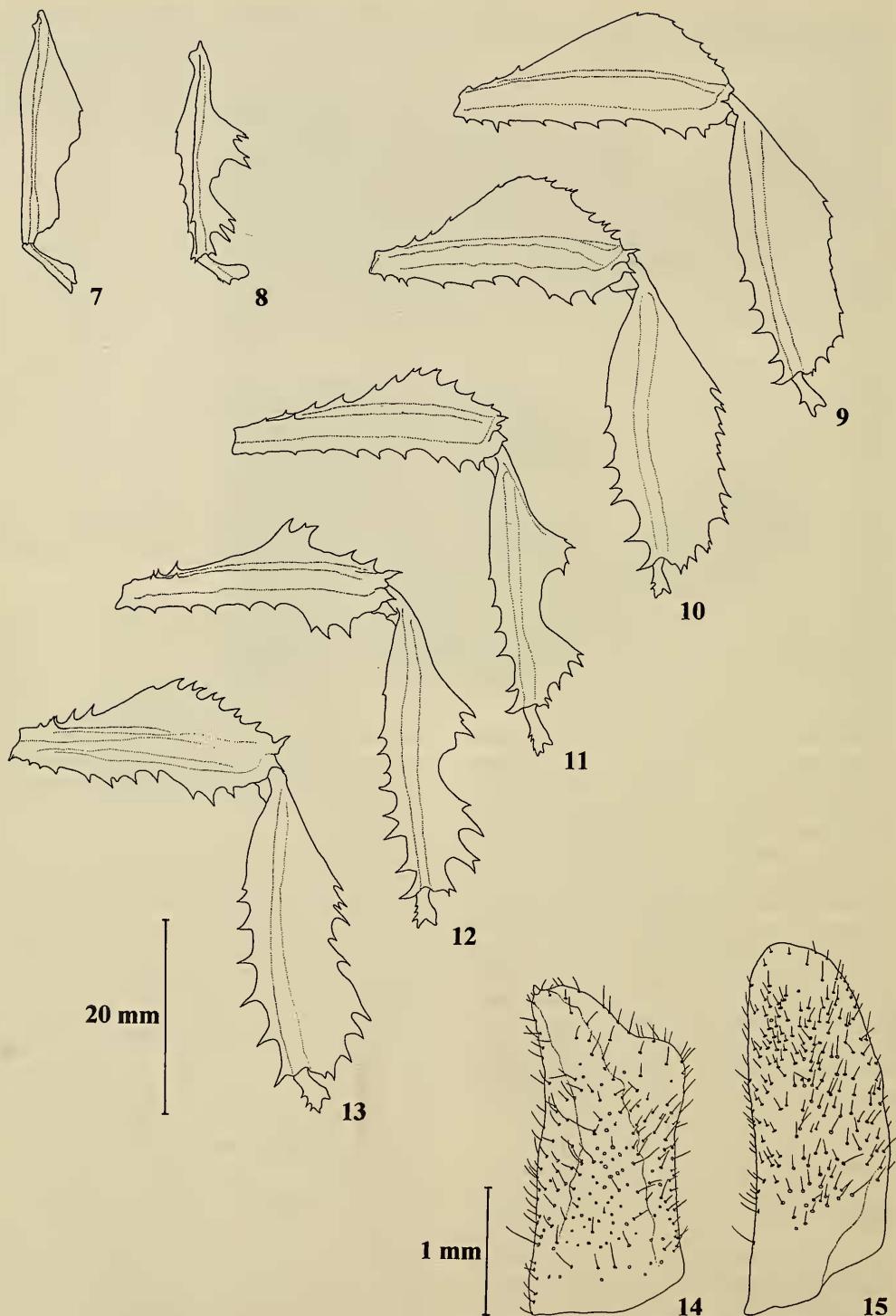
Egg (figs. 3-4). — Measurements given in table 2. Operculum conical. Chorionic membrane transparent, not thickened and modified into a capitulum on the operculum (see below). Capsule smooth and glossy, marked with mottled pattern of black and grey on cream. Micropylar plate cream, slightly raised above surface of capsule on micropylar mound, with lateral arm on either side of the micropylar cup region.

Etymology

This species is named in honour of Dr. Ulf

Table 2. Means, sample standard deviations and ranges of dimensions of 17 eggs from *E. carlbergi* holotype (1 egg taken from ovipositor, 16 extracted from abdomen). All measurements in mm (accurate to 0.01 mm).

Egg dimensions	$\bar{x} \pm SD$	Range
Total egg length	6.54 \pm 0.12	6.40 - 6.85
Capsule length	5.17 \pm 0.07	5.06 - 5.31
Capsule height	4.49 \pm 0.03	4.42 - 4.56
Capsule width (maximum)	3.79 \pm 0.05	3.71 - 3.84
Length of operculum	1.37 \pm 0.12	1.22 - 1.54
Diameter of operculum (maximum)	2.32 \pm 0.07	2.20 - 2.43
Micropylar plate length	6.09 \pm 0.28	5.70 - 6.73
Micropylar plate width (at middle)	0.67 \pm 0.03	0.61 - 0.70
Length of micropylar arm	1.74 \pm 0.06	1.60 - 1.79
Distance across micropylar arms	3.00 \pm 0.07	2.88 - 3.07
Height of micropylar mound	0.15 \pm 0.03	0.13 - 0.19



Carlberg, in recognition of his work on and passion for *Extatosoma*.

Biology and behaviour

In common with the other members of the genus, *E. carlbergi* is arboreal and when not feeding hangs motionless upside down under thin branches of the host tree (fig. 1). The holotype was collected on *Calliandra surinamensis* (Leguminosae), an introduction from South America commonly grown in PNG gardens (Verdcourt 1979). In captivity the specimen accepted *Leucaena* sp. (Leguminosae) and guava, *Psidium* sp. (Myrtaceae). Both originate from the Neotropics and the former is cultivated in Wau as a shade tree for coffee, while the latter is grown for its fruit. J. Somp (pers. comm.) informed the author that he has collected *E. carlbergi* on *Sterculia* sp. (Sterculiaceae), and *Casuarina* sp. (Casuarinaceae) is the only foodplant recorded on the data labels of this taxon examined during the course of this study.

Both *E. tiaratum* and *E. popa* are also polyphagous. The latter has been collected on *Casuarina*, *Diospyros ferrea* (Ebenaceae), *C. surinamensis* and *Hibiscus* sp. (Malvaceae) (taken from data labels listed in Appendix) and it will also feed on *Leucaena* and *Psidium* in captivity (pers. observation). For a list of the foodplants of *E. tiaratum* see Carlberg (1987b). The only foodplant known for *E. bufonium* is Japanese plum, ? *Prunus cerasifera* (Rosaceae) (from data label of adult female in Queensland Museum, Brisbane, Australia; collected at Mt. Tamborine, near Brisbane, December 1924).

When disturbed the *E. carlbergi* holotype was observed to exhibit a defensive behaviour similar to that shown by adult females of *E. tiaratum* (Carlberg, 1981) and *E. popa* (pers. observation). The abdomen is curled over the body, presenting the dense spination on the sternites towards the potential predator. The hind legs are raised and extended to reveal the aposematic pattern of black, white and ochreous bands on the ventral surfaces of the femur and tibia. This threat posture is maintained until any possible danger has passed. Should a predator approach too close, the insect will attempt to grasp it between the femur and tibia of the hind legs; retracting and extending the legs with a rapid, synchronous scissor-like action. The ventral margins of these appendages are furnished with sharp downwardly directed spines, which are capable of inflicting injury to human skin if caught between them.

The egg of *E. carlbergi* (figs. 3-4), which resembles

a seed, is held in the ovipositor for several hours and is then catapulted to the ground with a vigorous flick of the abdomen. Eggs of *E. popa* (A. J. E. Harman, pers. comm.) and *E. tiaratum* (Carlberg, 1984) are deposited in a similar manner.

ECOLOGY AND DISTRIBUTION OF THE EXTATOSOMA SPECIES

The known distributions of the two New Guinean *Extatosoma* species is shown in fig. 16. The locality records plotted on this map were taken from data labels of specimens examined by the author or from the literature. Records for *E. popa* are listed in the Appendix while those for *E. carlbergi* are listed under the species description. Dubious records or possible misidentifications have been omitted.

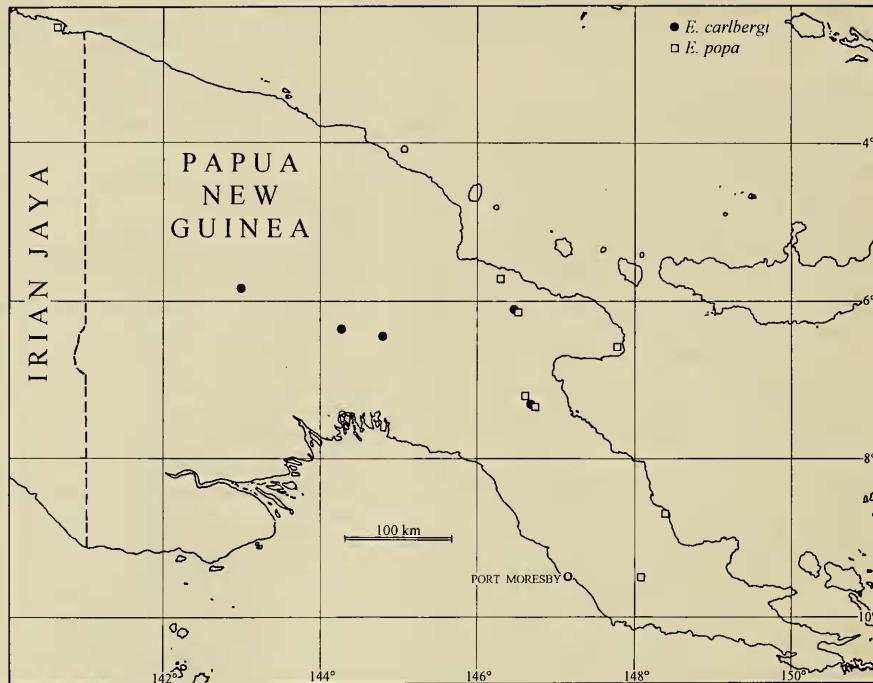
From fig. 16 it can be seen that *E. popa* has a wider recorded geographical distribution than *E. carlbergi*, ranging from Jayapura in Irian Jaya to Mt. Obree in the Owen Stanley Range, PNG. Altitude appears to be the most important factor in determining the distributions of these two species. Günther (1929) placed *E. popa* in an altitude band of 600-1500 m above sea level. However, the highest that this species has been recorded is c. 1200 m at Budemu, PNG. In contrast, all known specimens of *E. carlbergi* have been collected in the range 1100 m (Wau, PNG) to 1600 m (Tari, PNG). Wau (1100-1200 m) and Wantroat, PNG, (1200 m), where the species are sympatric, are located within the c. 100 m altitudinal overlap of the two species ranges.

The altitudinal ranges of *E. popa* and *E. carlbergi* match the distributions of two discrete vegetation belts, lower montane rain forest and mid-montane rain forest respectively, which differ from each other both in terms of species composition and in the structure and physiognomy of the vegetation. Lower montane rain forest has a mean canopy height of 30-40 m and is distinctly drier in aspect than the mid-montane, with few species of ferns and mosses. In contrast, the mid-montane rain forest has a mean canopy height of 20-30 m and its main characteristic is the abundance and high species diversity of terrestrial and epiphytic ferns, mosses and lichens (Johns 1982).

It is proposed that the gross differences in colour pattern and morphology seen between *E. popa* and *E. carlbergi* (nymphs and adult females only; adult males of *Extatosoma* are macropterous and differ from nymphs and adult females in both body form and behaviour) are the result of these species evolving cryp-

Figs. 7-15. *Extatosoma* spp. adult ♀ appendages. - 7-8, lateral views of left fore tibia and proximal tarsomere: 7, *tiaratum*; 8, *carlbergi* sp. n. (holotype). 9-13, lateral views of left hind femur, tibia and proximal tarsomere: 9, *tiaratum*; 10, *popa*; 11, *bufo-nium*; 12, *carlbergi* sp. n. (holotype); 13, *carlbergi* sp. n. (paratype from Tari, PNG). 14-15, ventral views of left cercus: 14, *carlbergi* sp. n. (holotype); 15, *tiaratum*.

Fig. 16.
Sketch map of Papua New Guinea and eastern Irian Jaya, showing known distributions of *E. popa* (13 records) and *E. carlbergi* (11 records).



sis adapted to different habitat types. Once evolved this would tend to restrict the species to the habitat in which it is best concealed from predators.

The body coloration of *E. popa* is primarily brown and when the insect is hanging under a branch at rest the foliose expansions of the legs (fig. 10) and abdomen give it a resemblance to a bunch of dried leaves. In the lower montane rain forests, where this species is found, dry brown leaves are presumably more common than in the wetter mid-montane forests occupied by *E. carlbergi*. In these latter forests, the bark of trees and other plants is covered by dense growths of lichens, and mosses are three times as abundant as in the lower montane (Johns 1982). Thus the dark green, white and black mottling of *E. carlbergi*, together with the arcuate flanges of the tibiae (figs. 8, 12) and small lateral expansions of the tergites (fig. 2), are probably adaptations for resembling foliose epiphytic lichens, such as the abundant *Usnea*, or leaves covered with epiphyllous growth.

The crypsis of the Australian *Extatosoma* mirrors that of the New Guinean species, with one, *E. tiaratum*, a leaf mimic (Brock 1992) and the other, *E. bufoninum*, a probable lichen mimic. Both taxa are restricted to the coastal forests of eastern Queensland and New South Wales (NSW), although the former species has doubtfully been recorded from Lord Howe Island (Redtenbacher 1908, Günther 1931). *E. tiaratum* is distributed from Daintree in north-east

Queensland (data from a final instar female nymph in BMNH) to Kiama, near Sydney, NSW (Froggatt 1922) and appears to range further inland than *E. bufoninum* (Beccaloni, unpublished). It is possible that literature records of '*E. tiaratum*' from Brisbane southward represent the undescribed taxon referred to earlier. *E. bufoninum* ranges from Moreton Bay, near Brisbane, south-east Queensland (data from a female nymph in BMNH) to Camden, near Sydney, NSW (Froggatt, loc. cit.). This species may also occur in north-east Queensland, as a female nymph probably belonging to this taxon was collected in Atherton in 1989 (P. D. Brock, pers. comm.). A patchwork of different forest types (ranging from rain forest to dry eucalypt woodland) is found in eastern Queensland and NSW and without further detailed study it is not possible to determine in which habitats the Australian *Extatosoma* live. However, considering the types of crypsis exhibited by these species, it is hypothesised that *E. bufoninum* will be found to inhabit a habitat type with a higher representation of lichens and other epiphytes than that in which *E. tiaratum* occurs.

COMPARATIVE MORPHOLOGY AND PHYLOGENETIC RELATIONSHIPS

The characters discussed below are taken from adult females and eggs, as only males of *E. popa* and *E. tiaratum* are known and they do not exhibit suffi-

cient characters to make comparisons worthwhile.

Both *E. popa* and *E. tiaratum* range from light to dark brown in colour, although the latter species is known to have a green form which is not uncommon. The dorsal foliose expansions of the femur and tibia of the legs (figs. 7, 9-10) are broad and well developed in both species, as are the lateral expansions of the fifth to seventh tergites (as in fig. 6). The lateral expansions of tergites two to four and eight to nine are reduced (*E. popa*) or obsolete (*E. tiaratum*).

The coloration of *E. carlbergi* and *E. bufonium* is again similar: both are green, with white and black mottling in varying proportions. The dorsal expansions of the tibiae (figs. 8, 11-13) are arcuate in both taxa and the lateral expansions of the fifth to seventh tergites (as in figs. 2, 5) are much reduced relative to those of *E. popa* and *E. tiaratum*. Lateral expansions of tergites two to four and eight to nine are relatively well developed.

The superficial similarities in coloration and body form (listed above) between *E. popa* and *E. tiaratum* and between *E. carlbergi* and *E. bufonium*, are probably due to convergence upon analogous cryptic morphologies and thus do not reflect the phylogenetic relationships of the group. Characters not obviously related to crypsis (see below) are incongruent with those characters involved in crypsis and suggest a grouping reflecting the biogeographical division of the taxa (New Guinea / Australia).

The New Guinean taxa share a number of features not possessed by the Australian taxa. Both are larger than the Australian species and the body spination is relatively longer and more robust. Both possess a distinctive pale v-shaped marking on the mesonotum, and the pair of medial lamellate spines on the posterior third of the meso- and metanotum are large and well developed. The paired medial lamellae of the fifth and sixth terga each occupy about one-third of the length of the segment and their basal width is less than their height (as in fig. 5). The posterior margin of the tenth tergite has large posteriorly directed spines (as in fig. 5) and the apex of the cercus is bilobed (as in fig. 14). The ventral expansion of the fore tibia has a denticulate margin (as in fig. 8) and the inner ventral margin of the median and hind femur is expanded ventrally towards its distal end (figs. 10, 12-13). The egg of *E. popa* (fig. 100 in Sellick, 1980) is virtually identical in appearance and dimensions to that of *E. carlbergi* (figs. 3-4).

The Australian taxa share the following characters: the pale mesonotal v-shaped marking (of *E. popa* and *E. carlbergi*) is absent in the adults (although present in newly hatched nymphs of *E. tiaratum*) and the pair of medial spines on the posterior third of the meso- and metanotum are poorly developed and, if double, are only weakly confluent basally. The paired medial

lamellae of the fifth and sixth tergites each occupy about one half of the segment and their basal width is greater than their height (as in fig. 6). The posterior margin of the tenth tergite has small posteriorly directed spines (as in fig. 6), which may be subobsolete, and the cercus is tapered towards its apex (as in fig. 15). The margin of the ventral expansion of the fore tibia is entire (as in fig. 7) and the inner ventral margin of the median and hind femur is only weakly (or not) expanded ventrally towards its distal end (figs. 9, 11). The eggs of *E. tiaratum* (fig. 8 in Clark, 1976a) and *E. bufonium* (pers. observation) share a number of characters not possessed by eggs of the New Guinean taxa. Eggs of both species lack micropylar arms and the opercula are only c. half the length (corrected for differences in egg size) of *E. popa* / *E. carlbergi* eggs. In addition, the chorionic membrane on the opercula of eggs of the Australian species is thickened and modified into an opaque hollow dome or capitulum. The chorionic membrane on the opercula of eggs of the New Guinean species is not modified into a capitulum, and instead is transparent and lies in contact with the surface of the operculum. (Note that the capitulum of *E. tiaratum* is relatively much larger than that of *E. bufonium*. Also note that the egg of *E. bufonium* is c. half the size of that of *E. tiaratum*, the capitulum is dark brown in colour and the egg capsule has a pitted and irregular surface. The capitulum of *E. tiaratum* is cream in colour and the egg capsule is smooth and glossy like the capsules of the New Guinean taxa).

It has not been possible to determine the polarity of the above characters, as appropriate outgroups to *Extatosoma* have not been identified. The other genera (e.g. *Podacanthus* Gray, *Tropidoderus* Gray, *Didymuria* Kirby) placed with *Extatosoma* in the tribe Tropidoderini, differ greatly from *Extatosoma* in both adult and egg morphology preventing useful comparison. However, the non-polar characters described above imply that either the two New Guinean species are sister taxa and/or the Australian species are sister taxa. This ambiguity can only be resolved through polarity determination.

Key to the adult females of *Extatosoma*

1. Mesonotum with conspicuous pale v-shaped marking; ventral expansion of fore tibia with denticulate margin (as in fig. 8) 2
- Mesonotum lacking a pale v-shaped marking; ventral expansion of fore tibia with entire margin (as in fig. 7) 3
2. Lateral expansions of tergites 5-7 small, non-overlapping (fig. 2); dorsal expansions of median and hind femur arcuate (figs. 12-13); body coloration pale green, with white and black mottling

..... *carlbergi* Beccaloni

- Lateral expansions of tergites 5-7 large and overlapping; dorsal expansions of median and hind femur broad, not arcuate (fig. 10); body coloration light to dark brown *popa* Stål

3. Tergites 2-4 and 8-10 bearing lateral expansions; dorsal expansions of median and hind femur arcuate (fig. 11); body coloration green, with darker green, white and black mottling *bufonum* Westwood

- Tergites 2-4 and 8-10 without lateral expansions; dorsal expansions of median and hind femur broad, not arcuate (fig. 9); body coloration brown or green, not mottled *tiaratum* (MacLeay)

ACKNOWLEDGEMENTS

This paper is based on the author's final year BSc (Hons) project, written while an undergraduate in Zoology at Imperial College (University of London). The author would like to thank Mrs J. Marshall and Mr J. Reynolds for assistance, advice and for enabling him to conduct much of his work in the BMNH. He is grateful to the following individuals for either sending him specimens or enabling him to examine material included in this paper: Mr S. Fellenberg (Sydney, Australia); Dr M. Hopkins (UPNG); Prof. R. Kumar (Department of Agriculture and Livestock, Port Moresby, PNG); Dr G. McGavin (Hope Dept. of Entomology, Oxford, UK); Dr G. B. Monteith (Queensland Museum, Brisbane, Australia); Dr M. S. Moulds (Australian Museum, Sydney, Australia); Dr H. Roberts (Forest Research Institute, Lae, PNG); Dr H. A. Rose (University of Sydney, Australia); Mr J. Somp (WEIC); and Mr J. S. Strazanac (BPBM).

The author's thanks also go to Mr P. D. Brock and Mr A. J. E. Harman (UK) for providing useful information, to Dr U. Carlberg (Sweden) for his enthusiasm and help, and to Jerry and Willie of Wau (PNG) for collecting the holotype of *E. carlbergi*.

The author is also very grateful to Mr P. E. Bragg (UK), Dr V. K. Brown (Imperial College, UK), Mr R. I. Vane-Wright (BMNH) and Dr M. Wilkinson (BMNH) for reading and commenting on the manuscript and he is indebted to all the organisations and individuals who approved and sponsored the 'Imperial College Expedition to Papua New Guinea 1990'.

REFERENCES

Bragg, P., 1991. Species census returns 1991. - Phasmid Study Group Newsletter 46: 6.

Brock, P. D., 1992. Rearing and studying stick and leaf insects. - The Amateur Entomologists' Society, Handbook 22: i-v, 1-73.

Carlberg, U., 1981. Defensive behaviour in adult female *Extatosoma tiaratum* (MacLeay) (Phasmida). - Entomologist's Monthly Magazine 116: 133-138.

Carlberg, U., 1983. Bibliography of Phasmida (Insecta) I. 1970-1979. - Spixiana 6: 27-43.

Carlberg, U., 1984. Oviposition behaviour in the Australian stick insect *Extatosoma tiaratum*. - Experientia 40: 888-889.

Carlberg, U., 1987a. Bibliography of Phasmida (Insecta) VI. 1980-1984. - Spixiana 10: 147-156.

Carlberg, U., 1987b. Culturing stick- and leaf-insects (Phasmida)-A review. - Zeitschrift Versuchstierkunde 29: 39-63.

Clark, J. T., 1976a. The eggs of stick insects (Phasmida): a review with descriptions of the eggs of eleven species. - Systematic Entomology 1: 95-105.

Clark, J. T., 1976b. The capitulum of phasmid eggs (Insecta: Phasmida). - Zoological Journal of the Linnean Society 59: 365-375.

Cogan, B. H. & K. G. V. Smith, 1974. Insects. - Instructions for Collectors 4a, 5th Edition, British Museum (Natural History), London, 169 pp.

Compton, S. G. & A. B. Ware, 1991. Ants disperse the elaiosome-bearing eggs of an African stick insect. - Psyche 98: 207-213.

Froggatt, W. W., 1922. Description of a new phasma belonging to the genus *Extatosoma*. - Proceedings of the Linnean Society of New South Wales 47: 344-345.

Günther, K., 1929. Die Phasmoiden der deutschen Kaiserin Augusta-Fluss-Expedition 1912-13. - Mitteilung aus dem Zoologisches Museum in Berlin 14: 597-746.

Günther, K., 1931. Beiträge zur Systematik und Geschichte der Phasmoidenfauna Ozeaniens. - Mitteilung aus dem Zoologischen Museum in Berlin 17: 753-835.

Gurney, A. B., 1947. Notes on some remarkable Australasian walkingsticks, including a synopsis of the genus *Extatosoma* (Orthoptera: Phasmatidae). - Annals of the Entomological Society of America 40: 373-396.

Harman, A., 1985. The genus *Extatosoma* Gray. - Phasmid Study Group Newsletter 25: 5.

Hughes, L. & M. Westoby, 1992. Capitula on stick insect eggs and elaiosomes on seeds: convergent adaptations for burial by ants. - Functional Ecology 6: 642-648.

Johns, R. J., 1982. Plant zonation. p. 309-330. - In: J. L. Gressitt (Ed.), Biogeography and Ecology of New Guinea. Junk, The Hague.

Redtenbacher, J., 1908, p. 380-381. - Die Insektenfamilie der Phasmiden 3. Verlag Von Wilhelm Engelmann, Leipzig.

Sellick, J. T. C., 1980. A study of the eggs of the insect order Phasmida with particular reference to the taxonomic value of egg structure in this group. - Unpublished Ph. D. thesis, University of London, England.

Verdcourt, B., 1979. - A manual of New Guinea Legumes. Kristen Press Inc., Madang, PNG, 645 pp.

Vickery, V. R., 1983. Catalogue of Australian stick insects (Phasmida, Phasmatodea, Phasmatoptera, or Cheleutoptera). - CSIRO Australia, Division of Entomology Technical Paper 20: 1-19.

Wilson, S. K., 1991. Throwing your babies at the enemy. - GEO Australasia's Geographical Magazine 12: 106-113.

Received: 25 May 1993

Accepted: 30 August 1993

APPENDIX

The following records of *Extatosoma popa* were used to plot fig. 16. The data have been taken from material examined by the author, unless stated otherwise. IRIAN JAYA: 1♂, Hollandia, 3°10'S 140°E, 300-600 m, i.1937-8, W. Stüber (BMNH). PAPUA NEW GUINEA: Madang Prov.: 1♀, Finisterre Mts., Damanti, 1065 m, 2-11.x.1964, M. E. Bacchus (BMNH); 1♀, Finisterre Mts., Budemu, c. 1200 m, 15-24.x.1964, M. E. Bacchus (BMNH); Morobe Prov.: 2♀, Wantroat, 1200 m, *Casuarina*, x.1957, R. W. Paine (BMNH);

2♀, Wau, golf course, 1150 m, ex *Calliandra surinamensis* Benth., 13.vii.1990, G. W. Beccaloni (BMNH); 1♀ (nymph), Wau, c. 1200 m, ex *Hibiscus*, 1.vii.1990, G. W. Beccaloni (BMNH); 1♀ (nymph), Wau, 1150 m, 24.vi.1974, Gewise Otaweto (WEIC); 1♂, Wau, 1180 m, 18.x.1974, A. D. Hart (WEIC); 1♂, Wau, 1150 m, coll'd on *Diospyros ferrea*, 6.xii.1975 (WEIC); 1♀, Bulolo, v.1990 (BMNH); Northern Prov.: 1♀, Mt. Obree, 1.x.1921, R. Neill (BMNH).

The following records were taken from Gurney (1947): PAPUA NEW GUINEA: Morobe Prov.: Sattelberg, vic. Finschafen; Northern Prov.: Buna.